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#### ON THE MORPHOLOGY OF THE ROTATORIAN FAMILY FLOSCULARIIDÆ.

BY THOMAS H. MONTGOMERY, JR.1

The thoughts which group themselves about the theories of larval homologies, and in particular that one which regards the trochophore stage as the recurrence or at least parallelism of an ancestral phyletic form, comprise one of the many inducements to investigate the anatomy of the Rotatoria. For it is generally maintained by those workers who uphold the trochophore theory in its logical sequences, that the adult Rotatorian and the trochophore larva show close similarities. One line of the approach, then, to test the correctness of the ideas of such larval homologies, is to extend our knowledge of the structure of A huge literature has grown up around this group of the Rotatoria. animals, but with the exception of a very few detailed monographs the writers have contented themselves with the description of the external form. This is the more remarkable since the Rotatoria lend themselves better than most forms, thanks to their great transparency, to the study of fine details of structure in the living animal.

Those who have not occupied themselves especially with the anatomy of this group make the common assumption that all Rotatoria show essentially the same type of structure. But this is erroneous for two reasons: first, because in Nature there do not occur types of structure, but gradations of structure; and second, because the Rotatoria evince very great differences among themselves. For the bearing of the group as a whole upon the views of larval homologies it is first necessary to examine the various Rotatorian groups comparatively, in order to determine which of them is the most generalized or primitive; then this group should be compared with the various kinds of trochophore This is a problem to be attacked from more sides than the purely morphological, for at once appears the striking fact that the Rotatoria are for the most part fresh-water forms, while the trochophore larvæ are characteristic exclusively of marine groups. Of the living Rotatoria, are the most primitive forms found in the sea or in fresh water? And of them, are the pelagic forms more primitive than

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the creeping and attached forms? Here again we are met with the fact that a knowledge of distribution, and its factors, constitutes a very important ally in the study of phylogeny.

The present paper is offered as a contribution to the morphology of the Flosculariidæ alone. The only thorough account so far of the anatomy of any species of this family is that of Gast on Apsilus lentiformis. The occurrence of Apsilus, Stephanoceros and four species of Floscularia during the past winter and spring in a pond in the garden attached to our zoological laboratory, enabled me to study all these forms at the same time, and so to make the desired comparison of them. But until I have had opportunity to examine for myself other families of the group, it would be premature to express any opinions upon the phyletic value of the Rotatoria as a whole.

In regard to the methods of study, the examination of the living animals under slight pressure of the cover-glass has proved the most important. Fixation with hot corrosive sublimate or with Flemming's fluid, and staining with hæmatoxylin or carmines were of value in rendering nuclei more distinct, but even in life all the nuclei of the body tissues can be seen. The preparations may be mounted in balsam with no shrinkage by passing the objects from the absolute alcohol through graduated mixtures of cedar oil with alcohol. Sections were made of Apsilus alone. The complete literature has been cited for Apsilus and Stephanoceros, but for Floscularia only such contributions as concern the internal anatomy.

#### APSILUS, Meczn.

#### HISTORICAL.

Leidy (1857) described very briefly *Dictyophora* nov. gen. *vorax* nov. sp., from the vicinity of Philadelphia. Mecznikow (1866) described *Apsilus* nov. gen. *lentiformis* nov. sp., from Giessen; he noted the complete absence of ciliary wreaths, form of the corona, the lateral antennæ, intestinal tract, musculature, nephridia, and mistook for the brain a large muscle; he described the male also. Then Leidy (1882) figured his species, and mentioned that it differs from the species of Mecznikow in the lack of lateral antennæ and of a ganglion. Forbes (1882) gave a crude figure of and briefly described *Cupelopagis* nov. gen. *bucinedax* nov. spec., from Illinois, describing the alimentary tract and the external form. Foulke (1884) described as a new species *Apsilus bipera*, from Philadelphia; the corona was described as a membranous hood or net, two stomachs (the proventriculus erroneously regarded as a stomach), lateral antennæ, musculature; she pointed out that the

name Dictyophora is preoccupied, and proposed to recognize as three distinct species Apsilus vorax (Leidy), A. bipera Foulke and A. bucinedax (Forbes). In rejoinder to this paper Leidy, in the same year, proposed to unite these under the name Apsilus vorax, and found at last the lateral antennæ. Hudson and Gosse (1886) placed vorax and bucinedax as synonyms of lentiformis, and bipera as a distinct species; they relegated this genus to the Flosculariida. Stokes (1896) gave a good description of bucinedax, from Trenton, N. J.; he described the lateral antennæ, æsophageal tube, long immobile setæ arranged in tufts upon elevations of the inner surface of the coronal cup, slender and numerous coronal muscles, an ovary extending across the whole width of the body. He also figures the corona of bipera from the same locality, and considers the four described species as all distinct. Lund (1899) held that the genus should be removed from the Flosculariida, and placed in a separate family near the Asplanchnida. Jennings (1900) figured the young of a species of Apsilus. Finally Gast (1900) has given a very detailed and accurate account of the anatomy and histology of a species he calls vorax Leidy (holding lentiformis to be synonymous), and regards bipera and bucinedax to be distinct from it.

Thus the European species, *lentiformis*, has been well described by Mecznikow and Gast, but of the three described American species the accounts, with the exception of that of Stokes of bucinedax, are so meager that the status of these is very perplexing. Foulke was right in uniting all these in the one genus Apsilus. A. bucinedax (Forbes) is well marked from all the others by the shape and great size of its germarium. Now the species which I shall describe is from the same locality as the forms described by Leidy and Foulke, and agrees with both of these in all essential particulars (these authors had overlooked the germaria, nephridia and foot, all the sense-organs except the lateral antennæ, and the œsophageal tube). Foulke considered her species to differ from Leidy's in possessing lateral antennæ (but these had been overlooked by Leidy), in ciliation of the corona (probably, as Gast has remarked, flame cells were mistaken for such ciliation), in more strongly developed muscular system, and in the external form. I am inclined to conclude that these differences are only apparent, due to the meagerness of Leidy's descriptions. Stokes stated that bipera differed from vorax in that the ventral margin of the corona is projected forward; but in the form described by me this margin shows considerable variations in form. Hence bipera (Foulke) had best be considered a synonym of vorax (Leidy); and the three clearly recognizable species may be distinguished as follows:

- (a)—Germarium very large, extending across the whole width of the trunk, œsophageal tube present, immobile setæ within the . bucinedax (Forbes). coronal cup, . . . . . . . . . . . . bucinedax (b)—Germarium small, rounded, no setæ within the corona. coronal cup, .
- - (1)—Esophageal tube present, dorsal cuticula of trunk with trans-
  - verse thickened ridges, . . . . . . . . . . . vorax (Leidy). (2)—Œsophageal tube absent, dorsal cuticula without such ridges, lentiformis Mecznikow.

In the description which follows I shall refer for comparison mainly to the description of Gast for lentiformis, since his account is by far the most thorough.

#### Anatomical.

The external form is fairly well known. The trunk is somewhat wider than high, rounded posteriorly, while anteriorly it is continued as a large corona (Rüssel, Mecznikow; cup, Leidy; net, Foulke; Mund-When fully extended the form is as shown in the trichter. Gast). figures (Pl. XVIII, 1-3), the corona very large and its aperture usually in the horizontal plane but sometimes oblique. The posterior wall of this aperture (mouth) may be rounded or notched, or may project forward as a convex lobe. On the ventral surface of the trunk is the rudimentary foot (Chitinring, Mecznikow; disk or sucker, Leidy; Fuss, Gast); and behind that, also ventral, the cloacal aperture. The lateral antennæ are clearly visible on the sides. The whole animal is so beautifully transparent that the greater part of the following description has been based upon a study of the living animal.

Hypodermis and cuticula.—The hypodermis is a very thin layer, with its flattened nuclei far apart; at the margins of the mouth it is only slightly thickened. The cuticula is thin, colorless, and (especially on the dorsal surface) covered with minute tubercles which may be ovoid or stellate (as Gast found). On the antero-dorsal surface of the trunk there are broad but narrow thickenings of the cuticula (Pl.XVIII, x, fig. 1), the number and exact arrangement of which is subject to considerable variation; each of these ridges bears tubercles. cuticula and hypodermis of the body wall are continued inward as the lining of the corona; there the minute tubercles are replaced by minute conical projections, borne mainly upon longitudinal ridges of the cuticula. The whole cuticula is very flexible, and when the animal is strongly contracted and the corona rolled inward it is thrown into many folds; radial folds are also found around the cloacal aperture. No cilia are found anywhere upon the surface of the body nor within the corona, nor yet any immobile setæ.

Alimentary tract.—The large cavity (Pl. XVIII, Inf., figs. 1-3) of the corona opens externally by the ventral mouth (coronal aperture). It is without cilia and lined by a continuation of the hypodermis and its cuticula. It is succeeded by a thick-walled short œsophagus (Pl. XVIII, Oes., fig. 1), also without cilia and with a sphincter muscle (as Gast has described.) From the esophagus, and attached to its posterior end, a narrow flexible tube (Pl. XVIII, Oes.T., figs. 1-3) extends back into the proventriculus, which may be termed the esophageal tube (this was also described by Stokes for A. bucinedax). tube is lined by a thin epithelium with a few nuclei, and its posterior slightly enlarged end is free; it is laterally compressed, and probably possesses a musculature of its own, since it beats in rapid undulations with many changes of form; it is very elastic to allow the passage of the large objects of food (mainly smaller free-swimming Rotatoria, also Ostracoda, Nematoda, Infusoria and Acarina). The proventriculus (Prov.) is a large, distensible sac, of nearly the width of the trunk; its interior surface is lined by a cuticula without cilia, next follows a clear zone of transparent protoplasm, then the peripheral cytoplasmic layer containing the nuclei. The musculature of this region described by Gast I was unable to find. The mastax lies at the posterior end of the proventriculus; its appearance is shown in fig. 1, and the masticating teeth of one side shown in fig. 5; I have not been interested to determine its finer structure, which has been done very carefully by Gast, but will simply state that its large tooth is not sharply bent at the tip as in lentiformis, and that of the four smaller teeth on each side one is frequently absent. Further, the usual parts may be distinguished: the unci and manubria, the fulcrum and its rami. On this follows the stomach proper (Chylusdarm, Mecznikow; esophagus, Foulke; stomach, Leidy; Magendarm, Gast). This (Pl. XVIII, Stom., figs. 1-3) is the only portion of the tract that is ciliated, and it is the assimilative portion of the intestine, with a single epithelium of large nucleated cells containing fatty globules. The posterior intestine (P.Int.) is a wide sac lined by a flat nucleated epithelium, which opens into the dorsal side of the cloaca (Cl., figs. 2, 3), a distensible tube lined by a similar epithelium. The cloacal aperture (Cl.Ap.) is surrounded by a sphincter muscle (found by Gast) and is actually ventral, but morphologically dorsal since it is behind the foot.

The only glands of the intestine are one pair of large stomach glands; these (Stom.Gl., figs. 1-3) are pyriform with long ducts, the body of each gland placed at the ventro-posterior margin of the posterior intestine, the duct curving up around the dorsal margin of the intestine to

join the stomach; each gland (which has been fully described by Gast) has one large nucleus, or as many as three nuclei evidently produced by amitosis of the single one. The substance of these digestive glands appears granular.

Foot.—This has been carefully described by Gast, and I have little to add to his description. It is immovably attached to the surface on which the animal rests by the secretion of large hypodermal glands which are apparent only in the free-swimming stage. Its outline (F., figs. 2, 3) is more or less circular and it is placed upon the ventral surface of the body anterior to the cloacal aperture, its margin slightly elevated.

Musculature.—A. vorax agrees very closely with A. lentiformis in the details of the musculature, which is very strongly developed. The following muscles may be distinguished (figs. 1–3):

- I. Hypodermal muscles (muscles attached at both ends to the hypodermis).
  - (a) Circular muscles.
- (1) Sphincter coronæ primus, Sph.C. I., a completely closed ring at the edge of the corona with a dorsal loop (Gast's rm 1).
- (2) Sphincter coronæ secundus, *Sph.C. II*, a narrower muscle just behind the preceding, interrupted ventrally (Gast's rm 2).
- (3) Sphincter coronæ tertius, *Sph.C. III*, a completely closed ring (Gast's rm 3a).
- (4) Sphincter coronæ quartus, Sph.C. IV, present only dorsally and not parallel to the other sphincters (Gast's mb of his fig. 2).
- (5) Sphincter coronæ quintus, *Sph.C. V*, a slender muscle interrupted dorsally and ventrally (Gast described it as a branch of his rm 3).
- (6) Sphincter coronæ sextus, Sph.C. VI, a completely closed ring (Gast's rm 4).
- (7) Sphincter coronæ septimus, *Sph.C. VII*, the largest of the coronal sphincters, a closed ring giving on each side a branch to join the next (Gast's rm 5).
- (8) Sphincter coronæ octavus, Sph.C. VIII, with a shorter dorsal and a larger ventral interruption (Gast's rm 6).
- (9) Sphincter trunci primus, *Sph.tr. I*, a small muscle, present on each side dorso-laterally only, subject to considerable variation.
- (10) Sphincter trunci secundus, *Sph.tr. II*, interrupted dorsally only (Gast's rm 7).
- (11) Sphincter trunci tertius, Sph.tr. III, interrupted ventrally and dorsally (Gast's rm 8).

- (12) Sphincter trunci quartus, Sph.tr. IV, interrupted dorsally but generally closed ventrally (Gast's rm 9).
- (13) Sphincter trunci quintus, *Sph.tr.*, *V*, dividing into three branches, interrupted dorsally and ventrally (Gast's rm 10).
- (14) Sphincter trunci sextus, *Sph.tr. VI*, paired, latero-ventral on each side of the foot (Gast's mb 3).
  - (b) Longitudino-circular muscles.
- (15) One pair, L.-C.M., passing from the posterior end of the body to about the middle of the trunk, then each turns ventrad (Gast's dlm 3).
  - (c) Longitudinal muscles.
- (16) Retractor coronæ primus,  $R.c.\ I$ , on the antero-dorsal surface of the corona (Gast's dlm 1).
- (17) Retractor coronæ secundus,  $R.c.\ II$ , on the postero-dorsal surface of the corona (Gast's dlm 2).
- (18) Retractor coronæ tertius, R.c. III, the innermost ventral pair, attached at the foot, passing forward and outward to insert upon Sph.C. I (Gast's vlm 1, but with a different anterior relation).
- (19) Retractor coronæ quartus, R.c. IV, paired, ventral (Gast's vlm 2).
- (20) Retractor coronæ quintus, R.c. V, inserted posteriorly at the sides of the foot, passing anteriorly to insert on Sph.C. I (it is much longer than Gast's vlm 3).
- (21) Retractor coronæ sextus,  $R.c.\ VI$ , paired, each with two branches ending posteriorly on the sides of the trunk, a single anterior branch inserting on  $Sph.C.\ I$ , and with two small lateral branches (which for the sake of clearness are not shown on the lateral view of the animal). (This corresponds more or less to Gast's vlm 4.)
- (22) Compressor trunci, C.T., paired, subject to considerable variation in form, a very thin but broad muscle always with several branches, extending back to the sides of the foot and anteriorly inserting upon R.c. III, R.c. IV, R.c. V.
- II. Visceral muscles (those which are entirely separated from the hypodermis, or in which only one end is attached to the hypodermis, which is the more usual condition).
  - (a) Circular muscles.
- (23) Retractor mastacis, r.m., paired, a short muscle connecting the side of the mastax with L.-C.M.
  - (24) Sphincter æsophagi, sph.oes. (found by Gast).
  - (25) Sphincter ani, sph.an. (found by Gast).
  - (b) Dorso-ventral muscles.
  - (26, 27) Depressor trunci primus et secundus, d.tr. 1 and 2, two pairs,

large muscles inserted on the hypodermis a little to one side of the foot, passing dorsally through the body cavity and inserted with enlarged ends on the hypodermis on the sides of the proventriculus (Gast's dv 1 and dv 2).

- (28) Depressor trunci tertius, d.tr. 3, paired, smaller than the preceding and placed posterior to them (Gast's dv 3).
- (29) Depressor trunci quartus, d.tr. 4, paired, behind the preceding (Gast's dv 4).
  - (c) Longitudinal muscles.
- (30) Levator coronæ, *l.c.*, paired, inserted posteriorly on the hypodermis at the sides of the mastax, passing through the brain in the wall of the corona, subdividing anteriorly, and ending on *Sph.C.* 1, *G.* (Gast's Lml 1).

(Gast's second visceral longitudinal muscle pair, his Llm 2, appears in vorax to be hypodermal, namely my R.C. V).

- (31) Deflexor coronæ, d.c., paired, arising dorso-laterally by two branches on the hypodermis, and passing forward to insert upon Sph.C. I (Gast's Llm 3 and Llm 4).
  - (d) Irregular muscles.
- (32) Contractor coronæ primus, c.c. 1, lying deep in the dorsal wall of the corona, a muscle with four arms (this is the one considered by Mecznikow to be a nerve ganglion; it corresponds to the mb of Gast's fig. 1).
- (33) Contractor coronæ secundus, c.c. 2, a muscle ring lying deep in the dorsal wall of the corona behind the preceding, with three pairs of lateral branches, and an unpaired medio-posterior branch (Gast's mbr).

Gast has described the histology of these carefully, and I have nothing new to add to his description.

Nephridial system.—This (Pl. XVIII, figs. 2, 3, 6) consists of the posterior unpaired canal opening into the cloaca, the lateral canals, and the ductules, the latter terminating each in a flame cell. Mecznikow and Stokes have described these organs fragmentarily, and Gast very fully.

The posterior canal (Pl. XVIII, figs. 2, 3) which opens into the anterior end of the cloaca (Cl.) is unpaired, thick-walled, with the lumen spirally twisted. At its anterior end the lateral canals join together, so that the terminal portion may be considered having originated by their fusion in the mid-line. Each lateral canal passes anteriorly, then bends dorsally (fig. 2), and has a very distinct lumen and a thin wall. Where the lateral canal turns dorsally it greatly enlarges in diameter to form a tripartite swelling; each of the three parts of this swelling possesses

one nucleus, and each is a single large cell containing a much convoluted, somewhat pulsatile lumen. The dorsal termination of this swollen portion lies at the boundary of corona and trunk, and at that point joins with the common nephridial ductule. From this ductule a secondary ductule passes anteriorly for a short distance, then divides into three tertiary ductules (figs. 1, 2, 6). The most median of these bears the first flame cell (Fl.C.1), and is connected with the corresponding ductule of the opposite side by a transverse commissure (fig. 1) placed above the mouth cavity. The middle tertiary ductule terminates in the second flame cell (Fl.C. 2). The most lateral tertiary ductule bends ventrad, then just behind the lateral antenna divides into two quartern ductules, the anterior of which is very short and terminates in the third flame cell (Fl.C. 3) placed near the lateral antenna, while the posterior passes backward and follows the course of the lateral canals of the nephridia, terminating in two short ductules each ending in a flame cell (Fl.C. 4, Fl.C. 5). Finally, from the common nephridial ductule pass backward on the dorsal surface of the trunk a pair of secondary ductules, each of which terminates in a flame cell near the mastax (Fl.C. 6). Gast's account differs in that he states that what I term flame cells 4 and 5 connect by short ductules directly with the lateral canals.

The nephridium of one side is thereby connected with that of the other at its anterior end by a commissure of the ductules, and at its posterior by fusion of the lateral canals. The only portion of the nephridia which are ciliated are the terminal flame cells; these (fig. 6) are completely closed from the body cavity, and each has an intracellular canal in which beats a long tuft of cilia (a typical "flame") attached at the wall of the cell where the lumen ends; the terminal end of each flame cell is somewhat enlarged, more or less amæboid, and contains one nucleus. The lumen of the ductules and of the lateral canals is also intracellular; a pair of nuclei are always present on the wall of the commissure connecting the anterior secondary ductules.

Germarium (Eierstock, Mecznikow; Keimdotterstock, Gast; ovary of Stokes) has the same relations as in *lentiformis*. It lies on the ventral side of the body (Ov., figs. 2, 3) anterior to the foot, often in an irregular position due to the pressure of embryos upon it, a small rounded mass of cells, with a distinct cellular lining which is continued backward as the unpaired oviduct (Ovd.) and joins the cloaca between the openings of the nephridia and the posterior intestine. It contains yolk cells (nurse cells) to the number of 10–14, large cells without distinct boundaries, each with a large nucleus containing a huge nucleolus.

A much smaller space is occupied by the much smaller germ cells, placed near the duct, characterized by very small, deep-staining nuclei and clear cytoplasm. Gast correctly noted these two kinds of cells and their differences. The egg cells do not reach their full size within the germarium, but only when they leave it and reach the oviduct, which becomes dilated by them to serve as a uterus for the complete embryonal development; as many as five large embryos are found in the uterus at one time, representing different stages of development.

Nervous system.—Stokes was the only one to see this organ complex before the time of the very thorough account by Gast. The cerebral ganglion lies in the mid-line above the alimentary tract (Pl. XVIII, Cer., figs. 1, 2), at the junction of corona and trunk or a little anterior to this point. Seen from the side (fig. 2) it appears ovoid, a little longer than high. Seen from above (Cer., figs. 1, 6) it is found to be widest in the transverse plane. Through each side of it passes a visceral longitudinal muscle (levator coronæ, l.c.). In life as well as in stained preparations the following nerves can be seen passing from this cerebral ganglion (figs. 1, 6). From its dorso-anterior edge three pairs of delicate nerves, which converge to the dorsal sense-organ (D.Sens.O.), i.e., pass upward and forward from the ganglion. Each of these nerves has a nucleus at the point where it joins the ganglion. From each side pass out at least eight nerves: one for the latero-anterior sense-organ (A.Sens.O); one for the latero-posterior sense-organ (L.Sens.O.); two large nerves which pass back from the latero-posterior angle of the ganglion but which could be traced only a short distance; and four other nerves which could be traced only a short distance, but one or two of which appeared to be connected with the nephridial tubules. The ganglion and its nerves are thus strictly bilaterally symmetrical.

Now the three pairs of nerves which can be traced to the three sets of sense-organs all arise from the dorsal margins of the ganglion; the dorsal portion of the ganglion may then be essentially sensory. The two large ventral posterior nerve pairs arise from two large cells, each evidently bipolar, placed at the ventro-posterior margin of the ganglion; Gast noted only one of these and only one posterior nerve. These two cells are characterized by their great size (they might be called on this account neurochord cells, with reference to similar huge cells in Nemertini, Annelida and Crustacea), and the large size of their nuclei. Since these differ so markedly from the demonstrated sensory nerves, it is very probable that they innervate either the musculature or the viscera, i.e., that they are either motor or splanchnic in function. Then since their roots are ventral in the ganglion, it would follow that

there may be a differentiation within the latter of a dorsal sensory and a motor or sphlanchnic ventral portion. The nerve cells in the brain are quite numerous and symmetrically arranged, but cell boundaries are distinguishable only in the case of the two huge cells. Two consecutive sections of one and the same ganglion are figured (figs. 7, 8), cut in an obliquely horizontal plane, one passing through the nerves to the lateral antennæ and one of the huge cells (fig. 8), and the other (fig. 7) passing further forward. In the latter can be seen what appears to be a transverse fibrous commissure on the ventral surface of the ganglion. The nerve cells are thus arranged mainly dorsally and posteriorly.

There are no recognizable nerve cells on the ventral surface of the alimentary tract, as far as can be determined by the usual staining methods.

Sense-organs.—The dorsal sense-organ (D.Sens.O., figs. 2, 6) is a specialization of the hypodermis on the dorso-midline of the corona, and was discovered by Gast. It consists of a group of cells (fig. 6) in which one large and five small nuclei can be seen, which compose a thickened area of the hypodermis, and above which there is a small annular thickening of the cuticula; no sense hairs were seen. The antero-lateral sense-organs, also discovered by Gast, lie each (A.Sens.O., figs. 1, 6) upon the side of the corona, as a thickening of its wall. Each consists of a cytoplasmic mass containing four large nuclei immediately imbedded in a more granular cytoplasm, while into a more hyaline cytoplasm extends a slender cylindrical rod from the cuticula; there are thus some differences from the relations in lentiformis. A single nerve, containing a nucleus at its junction with the cerebral ganglion, innervates each of these organs. The postero-lateral sense-organs (lateral antennæ) lie each on the side of the corona somewhat ventral near the junction of the trunk (L.Sens.O., figs. 1-3). To each passes one large nerve, with a large nucleus at its peripheral end; and as Gast also observed, the organ itself consists of a tubercular elevation of the body wall, and on the apex of this a cylindrical cuticular process, bearing a tuft of long, non-vibratile sense hairs (fig. 6); the base of the cuticular process is enlarged and extends below the hypodermis.

Body cavity, connective tissues.—The body cavity contains a clear fluid in which float masses, varying in number and size, of a brown color; these are non-cellular and probably represent bye-products of metabolism. The connective tissue elements are branched, naked cells with many processes, constantly changing their form and moving about through the body cavity. They are frequently found in close

connection with the walls of the nephridia, particularly with the anterior commissure.

The immature female.—The free-swimming female (fig. 4), just hatched from the egg, shows the following differences from the adult. The corona is represented simply by a circular hypodermal thickening bearing a row of vibratile cilia; and in the part of the trunk projecting anteriorly beyond this ring lie a pair of large red eyes (E.). The mouth (M.) is ventral, and the most anterior portion of the alimentary tract contains short cilia which do not extend out of the mouth aperture. The cerebral ganglion (Cer.) is much larger than in the adult. The whole hypodermis is thicker, and that portion of it lining the well-demarcated foot (F.) consists of about six huge cells (F.Gl.) which Gast has shown to be gland cells, by the secretion of which the animal firmly attaches itself. The surface of the foot disk is covered with long cilia. The musculature I have not drawn in this figure, but it is similar to that of the adult.

#### STEPHANOCEROS, Ehrb.

#### HISTORICAL.

Stephanoceros was discovered in 1761 by Eichhorn, and he later figured it (1775, according to Ehrenberg). O. F. Müller (1776) declared it to be a Tubularian, and Oken (1815) also placed it among the hydroids. Goldfuss (1820) first named it, calling it Coronella fimbriata. Since this generic term was preoccupied Ehrenberg (1832) changed it to Stephanoceros, and called the species Stephanoceros Eichhornii, which all later writers have followed. According to our present generally accepted rules of nomenclature, however, and in justice to Goldfuss, this species must be named S. fimbriatus (Goldfuss) and not S. eichhornii Ehrenb. Ehrenberg (1832, 1835, 1838) gave good figures of the animal, described the intestine, stomach glands (which all later writers seem to have overlooked), six longitudinal muscles, the ovary, and the flame cells (which he termed gills). Perty (1852) described as a new species S. glacialis, but this is generally held to be an abnormal individual of fimbriatus. Leydig (1854) added richly to the knowledge of its anatomy and development. He was the first to note the nucleated hypodermis, circular muscles (he stated there are four longitudinal muscles in the foot which divide dichotomously), the esophageal tube, cilia in the coronal cup and intestine, lateral canals of the nephridia (with Ehrenberg he regarded these organs as respiratory). Gosse (1855) described minutely the mastax, and in 1862 gave quite a full account of the structure; by experiment he proved the nephridia to be excretory and not respiratory, found the contractile vesicle, four flame cells on each side of the body, described the dorsal glandular mass (found by Leydig) as the brain, and described five pairs of longitudinal muscles. Cubitt (1870) found the lateral sense-organs, but made the serious error of supposing that each of them was connected with a flame cell (his pulsatile sac), and supposed them to be respiratory structures for taking water into the nephridial tubules; he carefully described the ciliary wreath within the coronal cup, but mistook (like Leydig and most of the later describers) the dorsal glandular body for Hudson and Gosse (1886) gave very good figures; found five flame cells on each side of the body, described the connection of the lateral canals with the contractile vacuole, discovered the dorsal sense-organ, and described six pairs of longitudinal muscles. Vallentin studied stained sections; he found that large hypodermal cells of the foot secrete the tube; that the dorsal mass is not nervous but glandular and opens by a duct into the vestibule; he regarded the large hypodermal cells at the bases of the arms to be nerve cells. The male of this species has been described by Western (1893) and more carefully by Dixon-Nuttall (1896). Less important are the papers of Dujardin (1841), Weisse (1845), Dobie (1854), Pritchard (1861), Cubitt (1869), Peirce (1875), Rosseter (1881, 1884), Lord (1885), Jennings (1894, 1896, 1900, all faunistic).

#### ANATOMICAL.

Nothing new can be added to our knowledge of the external form (Pl. XIX, fig. 16). The margin of the corona is prolonged into five long arms, which are slightly flattened and extensile. These arms are slightly curved, and the dorsal, unpaired one slightly longer than the others. The body is long and slender, rather strongly demarcated from the long foot which ends in a short peduncle (fig. 14). The gelatinous tube (Tub.) is very transparent, with annular folds, elastic and of great thickness.

Hypodermis.—The hypodermis (Hyp., figs. 9-11) of the trunk is a thin layer with flattened nuclei. At the margin of the corona it is much thickened, so as to form at the base of each of the arms a mass of four or five large rounded nucleated cells. The hypodermis of the arms is about as thick as that of the trunk, but neither in the living state nor upon preparations in which the nuclei of other regions of the hypodermis are stained very sharply are nuclei to be found in it. The hypodermis of the arms of the corona would therefore appear to be a direct continuation of the cytoplasm of the large hypodermal cells at the

base of the arms. Each of these cells then has a great extent, from its base to the free tip of an arm. When the arms are fully extended the outlines of the hypodermis seen on optical section appear even, without any irregularities. But when the arms are partially retracted, the hypodermis appears partitioned into circular areas on its inner surface; on surface view these are seen as in fig. 13; and on optical section as in fig. 12. At first I was inclined to consider these as representing component small cells of the hypodermis, but the absence of nuclei in them excludes that view and they can be regarded only as folds of the continuous hypodermis due to the contraction of the arm. The arrangement of the cilia upon the arms is very complicated and has not yet been satisfactorily determined; it is best seen on a living arm in a contracted condition. On the outer as well as upon the inner surface of each arm the arrangement of the cilia is shown by the dotted lines in fig. 12; there the cilia are arranged in single rows, making angles together, these single lines of cilia separated by spaces which are without cilia. But on lateral view each arm shows a different arrangement of the cilia; here (fig. 13) the cilia are arranged in tufts placed on oblique thickenings of the surface of the hypodermis. In this figure only those cilia seen in profile are drawn in extenso, while the insertion points of those on the aspect of the arm toward the observer are represented by stippling. each patch of fine dots denoting a tuft of cilia. At the tips of the arms the cilia are more evenly arranged along the whole hypodermis. appearance of the tufts of cilia, arranged in oblique bands, are shown for the two ventral arms under a lower scale of magnification in fig. 16. The cilia are extensile, and in fully expanded condition attain a length considerably greater than that of the arms themselves; but this is to be seen generally only when the animal is under the pressure of a cover-I could not determine the presence of a cuticula upon the arms.

The hypodermis of the foot is thickened, and at the junction of this region with the trunk (figs. 9, 10) certain cells are very prominent. These may correspond to the foot glands of the other *Rotatoria*, and secrete the substance of the tube in which the animal lives. The short peduncle (fig. 14) by which the foot is attached probably represents a secretion of hypodermal cells at the distal end; this peduncle is short, hard and homogeneous.

Alimentary tract.—By an oblique diaphragm (Dia., figs. 9, 10) the cavity of the corona is divided into a more spacious infundibulum (Inf.) and a more posterior vestibulum (Vest.), both of which have a nucleated lining similar to that composing the hypodermis. The diaphragm is

an annular fold composed of a more thickened cell layer; it is shown in oblique ventral view in fig. 11, on lateral view in fig. 9, and on dorsal view in fig. 10. The drawings show that this ring fold bears cilia along the anterior border of its ventral half, a tuft of longer cilia on each side, while the margin of its dorsal half has no cilia. Only this diaphragm bears cilia, and none are found upon the walls of the infundibulum and vestibulum.

By a narrow aperture there follows upon the vestibulum the esophageal tube (Oes. T.), the distal end of which projects freely without attachment into the cavity of the proventriculus. This is an elastic tube that beats rapidly in many dilations and therefore probably possesses a musculature of its own; I could not determine nuclei in its The proventriculus (*Prov.*) is the largest portion of the alimentary tract, its wall composed of a single epithelium of large cells with distinct nuclei, and lined internally by a cuticula. In this posterior part lies the mastax, concerning which it will suffice to refer to fig. 18, a dorso-posterior view. Gosse was wrong in considering it to be rudimentary, for it has well developed unci and manubria, fulcrum and rami. The stomach (Stom.) is a rounded, dorsally placed sac lined by large cells which bear numerous long cilia. The posterior intestine (P.Int.) follows, lined by a flattened epithelium without cilia and with distinct nuclei; and behind it a very short rectum opening into the cloaca (Cl.).

A single pair of large stomach glands (Stom.Gl., figs. 9, 10) are present, each latero-ventral at the junction of proventriculus and foot, and each containing several nuclei.

Musculature.—The following longitudinal visceral muscles run from the foot through the body cavity of the trunk to attach themselves to the bases of the arms of the corona (figs. 9-11). One pair to the dorsal arm, extending to its outer sphincter muscle. A pair of dorso-lateral muscles, each of which inserts anteriorly on the thickened hypodermal ring of the corona at the junction of the dorsal with a lateral arm. And a pair of ventro-lateral muscles, each of which, when reaching the thickened hypodermal ring of the corona, divides into two branches which pass forward to the outer sphincter muscle of the coronal arms. Thus I find only three pairs of longitudinal muscles. All these muscles have their muscle bodies with nuclei contained in the foot. Of the circular hypodermal musculature, there are a large number of delicate sphincters in the foot and trunk region, and at the anterior end of the corona two sphincter muscles of large size (Sph.C. I and II, figs. 9-11). The remaining complicated network of musculature of the corona I have not studied.

Nephridial system.—The whole nephridial system of one side of the body is shown in fig. 9, and a portion of it from dorsal view in fig. 10. Into the posterior end of the cloaca (Cl.) opens the unpaired contractile vacuole (Con.V.); and into this a long elongate unpaired sac with distinct outer lining and containing a convoluted tube with wide, pulsatile lumen, the common terminal canal. At the free end of the latter unite with it the two longitudinal canals of the nephridia. Each of these passes forward latero-ventrally to about the level of the stomach glands, and there becomes much convoluted so that the exact course is difficult to follow; but through all these convolutions it remains a single tube with distinct walls. Each lateral canal then turns dorsad to about the position of the cerebral ganglion where it again becomes convoluted; its diameter is greatest in this portion of its course. At this anterior end the ductules are given off to the flame cells, and, as fig. 9 shows, one ductule passes forward and divides into five ductules. each ending in a flame cell (Fl.C. 1, Fl.C. 2). A second ductule passes posteriorly and ends in a flame cell (Fl.C. 6) placed near the stomach. In one individual I saw two other flame cells (Fl.C. 7, Fl.C. 8) placed near the sixth flame cell, but their connections with the ductules of the nephridial system I did not find. As the dorsal view, fig. 10, shows, in front of the cerebral ganglion a transverse commissure connects the ductules of the two sides of the body. Each flame cell (fig. 15) bears internally a flame of long cilia, and appears completely closed from the body cavity. The lumen of all the ductules and the main canals is intracellular, and cilia are found only in the flame cells. The whole nephridial system is exceedingly distinct in life, provided the animal is well expanded.

Dorsal glandular organ.—On the dorsal side, at the junction of the corona with the trunk, lies a large mass (D.Gl., figs. 9, 10) of clear vacuolar structures, which has been heretofore regarded by most writers as the brain. It is composed of clear transparent globules, varies in size in different individuals, and becomes shrunken by the action of alcohol. Nuclei are to be seen at its margins, particularly posteriorly, but I was unable to determine whether each of its component globules represents a cell. This organ is closely attached to the dorsal hypodermis around the dorsal sense-organ (D.Sens.O., fig. 9), and is penetrated by the nerves which pass to the latter from the cerebral ganglion (Cer.); it has no connection with the alimentary tract. The functional significance of this organ is wholly obscure, and I have supposed it to be glandular simply on account of its connection with the hypodermis and the dorsal sense-organ. It is not

probable that it forms the secretion for the tube, since it is of very large size in those large individuals with fully-formed tubes.

Germarium, oviduct.—The germarium (Ov., figs. 9, 10) is a more or less spherical organ placed on the ventral side of the body, composed of a syncytium (fig. 17) containing fully fifteen large nuclei which are nurse cells (yolk cells), and with at one end much smaller nuclei (ovogonia). The whole is surrounded by a nucleated membrane which is continued as a thin-walled unpaired oviduct (Ovd.) to open into the ventral surface of the cloaca between the rectal and the nephridial openings. One ovum matures at a time within the germarium, then is discharged into the oviduct which serves as a uterus for its further development until it reaches the free-swimming stage. As many as four or five embryos are to be found at once in the uterus.

Nervous system.—Most of the preceding writers have mistaken the dorsal glandular body for the ganglion, while Vallentin recognized this body as glandular, but supposed it to open by a duct into the alimentary canal, and considered the large hypodermal cells at the bases of the arms to be nerve cells. The cerebral ganglion (Cer., figs. 9, 10) lies directly below the dorsal glandular mass, is elongate from side to side and approximately cylindrical on lateral view. On stained preparations I could determine that it is composed of many small nerve cells, the nuclei of which stain deeply. On lateral view of the expanded living animal (fig. 9) the following nerves are seen to arise from it: (1) One pair which passes directly dorsad or dorso-caudad to innervate the dorsal sense-organ (D.Sens.O.); this pair penetrates the dorsal glandular body, and probably represents what Vallentin mistook for a glandular duct leading into the vestibulum. (2) A pair of nerves to each lateral sense-organ (L.Sens.O.). (3) An unpaired, very delicate median nerve to the dorsal hypodermis behind the dorsal sense-organ. (4) A pair of nerves which pass backward upon the sides of the proventriculus (Prov.). And (5) a pair of nerves, the largest of all, which pass ventrad on the sides of the proventriculus. I have found no evidence that the large hypodermal cells at the bases of the arms are nervous; the long fibres which Vallentin found proceeding from them probably represent the continuations of these cells to form the walls of the arms.

Sense-organs.—Eyes were seen only in one individual, a pair of small red spots (E., fig. 9), lying close to the cerebral ganglion. The dorsal sense-organ (D.Sens.O., figs. 9, 10) is a slight thickening of the hypodermis bearing a tuft of short sense hairs, which penetrate a circular aperture of the cuticula. Each lateral sense-organ (L.Sens.O.) has

one conspicuous large nucleus, and likewise bears a tuft of short cilia.

The body cavity is voluminous in the trunk and the foot (but does not continue into the peduncle of the latter). In it are free-floating, non-cellular corpuscles, probably waste products. The cavity of the arms is continuous with that of the trunk (figs. 9–11). Very few connective tissue cells are present in the body cavity.

# FLOSCULARIA, Oken.

#### HISTORICAL.

Of the numerous writers upon this genus only the following have considered to any extent the internal anatomy: Ehrenberg (1834, 1838) wrote with all the enthusiasm of the naturalist: "Sie sind einzeln, wie seltene schöne Blumen auf einer Wiese, und erfreuen gleich ihnen das Auge des Beobachters." He found the mastax, œsophageal tube and the stomach glands. Dobie (1849) gave a careful description with good figures, and distinguished the infundibulum, vestibulum and proventriculus; he saw the cilia on the diaphragm. Leydig (1854) added to this description in finding the contractile vacuole and the longitudinal muscles. Gosse (1855) described in some detail the masticatory apparatus; and (1862) erroneously termed a vascular system the narrow spaces of the body cavity in which float excretory corpuscles. The account of Moxon (1864) is much more thorough than any of the preceding, and contains the discovery of the dorsal and lateral antennæ, correct position of the cilia within the infundibulum, and occurrence of the nephridia with four flame cells on each side of the Cubitt (1869) studied particularly the cilia within the coronal The papers of Grenacher (1869) and Cubitt (1872) added little new. Eckstein (1884) gave a careful account of the hypodermis, and the muscles and peduncle of the foot. Hudson and Gosse (1886) add but little to the account of Moxon. The paper by Hood (1895) I have not seen. The males have been described by Hudson and Gosse and by Weber (1888). But the best of these descriptions, those of Dobie and Moxon, leave much untouched in regard to the finer anatomy.

#### Anatomical.

F. campanulata Dobie (Pl. XX, figs. 27–35; Pl. XXI) was the species obtained in the greatest numbers, and on this account its anatomy could be more fully determined than that of the others. F. conklini Montg. (figs. 25, 26, Pl. XX) was obtained at the same time, but it is rather a difficult form to investigate on account of the large number

of minute floating corpuscles within the body cavity which greatly obscure the internal organs. *F. coronetta* Cubitt (Pl. XX, figs. 22–24) and *F. ambigua* Hudson (Pl. XIX, figs. 19–21) were the other species studied, but *ambigua* in only a few individuals, so that for this species my observations are unfortunately fragmentary.

General form.—In all Floscularians there may be distinguished the corona, trunk and foot (Pl. XXI, fig. 37). The corona is in anterior extension and enlargement of the trunk. In campanulata (Pl. XX, figs. 27, 28, 31) it is largest, widely bell-shaped and prolonged into five broad lobes, the dorsal of which is largest and longest, next the two ventral lobes, and smaller than these the two lateral lobes. species the corona is subject to considerable individual variations in form, but is always much wider and fully as long as the trunk. In ambigua (Pl. XIX, fig. 20) the corona is relatively smaller, and of its five lobes the lateral pair are usually very small and often distinguishable only by the cilia which they bear. In conklini (Pl. XX, figs. 25, 26) the corona is more cylindrical, frequently considerably less than half the length of the trunk, the lateral lobes also very small. In coronetta (Pl. XX, figs. 22, 23) the lobes are more cylindrical and narrowed, with enlarged (knobbed) tips, the dorsal one only slightly longer than the others.

The trunk is elongate and cylindrical, in conklini (fig. 25) more arched on the ventral than on the dorsal side. The foot is an elongate proximal extension of the body, relatively longest in conklini and coronetta. The foot ends in a peduncle by which the animal is firmly attached to the surface of a water plant stem. This peduncle is much longer than broad in campanulata (Pl. XXI, fig. 40) and ambigua, little longer than broad in coronetta (Pl. XX, fig. 24), and fully as broad as long in conklini (fig. 26). These different species were all found attached to Myriophyllum, but to different parts of it, campanulata always to the very finest outgrowths of the plant; conklini usually to the angles at the bases of stems; ambigua and coronetta to larger stems.

In all these forms the animal is surrounded by a gelatinous, elastic tube (Pl. XXI, fig. 37, Tub.), with an anterior opening; in conklini (Pl. XX, fig. 26) the tube is relatively largest and its outer surface often covered with foreign particles, and in campanulata it is exceedingly transparent and usually without any such adherent particles. By a weak solution of methylene blue the tube quickly becomes colored intensely; and this method of demonstrating it shows its form with great distinctness.

The animals are highly contractile, thanks to the strongly developed

longitudinal muscles; the coronal lobes may be folded into the infundibulum, the whole corona and trunk much shortened, and the foot so contracted that its peduncle is brought close to the trunk.

Hypodermis.—The hypodermis of the trunk is a thin, one-layered epithelium, with relatively few nuclei (Hyp., figs. 20, 22, 23, 25, 27, 28). It bears a hyaline, structureless cuticula (Cut.). On the free margin of the corona it is much thickened and contains large nuclei which are easily seen even in life. In campanulata (Pl. XX, figs. 27, 28) this coronal thickening follows the margin of each lobe, and at the tips of the dorsal and ventral lobes are particularly large nuclei. That is also the case with ambigua (Pl. XIX, fig. 20). In conklini (Pl. XX, fig. 25) the dorsal lobe has the hypodermis thickened only at its tip. In coronetta (figs. 22, 23) the hypodermal thickening forms a ring around the base of the lobes, while the hypodermis forming the walls of the lobes is but little thicker than that of the trunk; this is an approach to the condition in Stephanoceros, and will probably be found to be the case in all forms where the lobes are slender. Another peculiarity of coronetta is that the cuticula covering the lobes is thicker than elsewhere upon the body; in the other species I could not distinguish with certainty a cuticula upon the lobes, though probably a delicate one is present.

The cilia of the external surface are limited in the adult to the margins and lobes of the corona. In conklini (figs. 25, 26) these cilia are no longer than the corona, and strongly vibratile; they are found also only upon the tips of the lobes. In coronetta the tip of each coronal lobe bears a tuft of long cilia (fully as long as the trunk), which have a slow undulatory movement; while the sides of the lobes and the interlobular margin of the corona bears much shorter cilia with a more rapid movement. In campanulata (Pl. XXI, fig. 37) the cilia fringe the whole free margin of the corona. Here they are longest upon the tips of the lobes, but all have a length greater than that of the corona and trunk together, and sometimes nearly two-thirds that of the entire The cilia in this species are non-vibratile, or at most with slight undulatory movements, and toward their free ends become gradually exceedingly tenuous. All preceding authors have figured them much too short, probably because their full length can be determined only with high powers of magnification. These cilia are less like true cilia than like the tenuous, stiff pseudopodia of Heliozoa; and like the latter they are extensile and retractile to some degree at least, as is shown by a protoplasmic flowing. They serve not to obtain food particles by ciliary currents, but rather as a wide basket to encompass the

prey. Generally they are held stiff and rigid; but at times wave-like undulations are seen to pass slowly along them. Unlike a heliozoan pseudopodium there is no supporting axial filament within them. Ambigua has cilia like those of campanulata, and also fringing the whole coronal margin. In these two species and in coronetta the cilia project out of the anterior end of the body in a thick tuft when the animal is strongly contracted.

In the foot the hypodermis is thicker than in the trunk, composed of larger cells. Its cells are largest at the junction of the trunk with the foot (Pl. XIX, fig. 20; Pl. XX, 22, 23, 25, 27, 28); and these may be gland cells which produce the gelatinous tube. The peduncle (figs. 24, 40) is homogeneous without cells or nuclei; it probably represents a secretion of certain large hypodermal cells found in the embryo but absent in the adult, which are placed at the distal end of the foot (Pl. XXI, fig. 38). The peduncle is firmly attached to the plant stem, so securely that when the animal is torn loose from its tube the peduncle is often left still attached.

Alimentary tract.—The following regions are marked in all the forms: infundibulum, vestibulum, œsophageal tube, proventriculus, stomach, posterior intestine, rectum, cloaca.

The infundibulum (Inf., figs. 20, 22, 25, 28) is the cavity of the anterior portion of the corona, and its opening to the exterior constitutes the broad mouth. It is lined by a thin one-layered epithelium in which nuclei can be distinguished by staining, is without cilia, and its wall is separated from the hypodermis to which it is attached only at its anterior margins, by the body cavity. The infundibulum is partially bounded off from the vestibulum behind it by the diaphragm. (Dia., figs. 22, 23, 25, 27, 28) is a thickened annular fold of the internal wall of the alimentary tract, and the only portion of the latter anterior to the stomach which is ciliated. Viewed from in front, i.e., from the mouth opening, it appears circular with a knob-like thickening at each side in campanulata (fig. 31). Each of these knobs bears a tuft of long and slowly vibratile cilia, while the border of the diaphragm ventral to these knobs bears a semicircle of very short and delicate, rapidly vibratile cilia. There are no cilia dorsal to the knobs. (fig. 25) the relations are in general similar. In coronetta (figs. 22, 23) the dorsal free margin of the diaphragm is considerably thicker, and bears short pointed projections (like those within the infundibulum of Apsilus); while the ventral margin bears rather long cilia upon several knobs. In all these species (I did not determine the relations in ambigua) the cilia appear usually to beat forward, i.e., into the infundibulum, but frequently they point backward and beat in the vestibulum. The latter (*Vest.*, figs. 20, 22, 23, 25, 27, 28) is the portion of the alimentary tract placed at the base of the corona, at the junction with the trunk; its lining is like that of the infundibulum.

Attached to the narrowed posterior aperture of the vestibulum is a slender tube, the esophageal tube, (Oes.T., figs. 20, 22, 23, 25, 27, 28), which extends back without posterior attachment into the proven-This tube is very thin-walled, and constantly moves in rapid undulations and distortions, so that its shape can be made out only when it comes to rest. Nuclei could not be determined in its walls in life, and all fixatives preserve it as poorly as they do the nephridia; so that stained preparations did not help in understanding its structure. But very delicate spirally arranged muscle fibrils compose a part of its wall; and it is probable that it possesses a nerve center of its own since it continues to beat after the other organs have ceased to live. In a state of rest (figs. 34, 35) it is cylindrical with a posterior enlargement, and a very small posterior aperture into the proventriculus. is very elastic to allow the passage of large objects of food (Infusoria and Mastigophora in the species studied), and may sometimes be everted anteriorly into the vestibulum.

The proventriculus (Prov., figs. 20, 22, 23, 25, 27, 28) is a large sac lined by a rather thick epithelium, with readily distinguishable nuclei; its internal surface is bounded by a delicate cuticula. At its posterior end lies the mastax (Mast.). This consists of chitinous, jointed parts, the manducatory apparatus, and of musculature for their movement. Gosse (1855) holds that Stephanoceros and Floscularia have no mastax in the sense that this term is used for other Rotatoria, i.e., that in the Floscularida it is not a special portion of the alimentary tract with a lining of its own. But it is surely homologous with that of the other groups, and though relatively very small I find it is not rudimentary but possesses all the characteristic parts found in the other Rotatoria. Thus in campanulata (Pl. XXI, fig. 39) the manubrium consists of two teeth, together constituting the uncus (Un.), and of a basal piece, the manubrium (Man.). A broad chitinous plate belonging also to the malleus lies below the uncus. The incus consists of a median fulcrum (Ful.) and of lateral rami (Ram.). The musculature is difficult to determine in its exact arrangement, so that I have not drawn it, but is readily seen in the living animal. The organ then has a special lining, the musculature, and is truly a mastax in the sense of Gosse, even though it does not form a separate compartment of the alimentary tract; and this is the case also in Stephanoceros and Apsilus.

The stomach (Stom., figs. 20, 22, 25, 27, 28) is thick-walled, with large cubical cells bearing long cilia; this is the assimilative portion of the intestine, and its cells are more or less filled with globules. Upon it follows the posterior intestine (P.Int.), lined by a thin-walled, nucleated epithelium without cilia. Here the fæces form large food balls in ambigua, but not in the other species. By a short rectum (Rec.), often barely distinguishable from the posterior intestine, an opening into the cloaca (Cl.) is attained. The cloaca is ciliated apparently only in coronetta (figs. 22, 23), is very thin-walled, and opens to the exterior by the cloacal aperture placed dorsally at the junction of the trunk and the foot, or a little anterior to it. The diameter of the different portions of the alimentary tract is dependent upon the amount of food contained in them.

One pair of stomach glands (Stom.Gl., figs. 20, 22, 23, 25, 28) is present in all the species, placed latero-ventrally at the boundary of stomach and proventriculus. In coronetta (figs. 22, 23) and ambigua (fig. 20) each gland is elongate with a single large nucleus, in conklini (fig. 25) pyriform with several nuclei, in campanulata (fig. 28) of the same shape but with one nucleus. The connection of these glands with the stomach was determined positively only for ambigua, but there can be doubt that they discharge into the stomach and not into the proventriculus in the other forms also.

A peculiar structure was found in every individual of ambigua, but in none of the other species. This was a body of a brown color (X.Y., fig. 20) placed in the posterior intestine, with a thick wall, a deep-staining body (nucleus?) in this wall, and rather vacuolar contents. It appeared to lie within the posterior intestine. It can hardly be a parasite, since exactly one of these bodies was found in the same region in each individual.

Musculature.—An exhaustive study of the musculature, such as was given for Apsilus, was not attempted for Floscularia. Of the hypodermal musculature (the following description applies particularly to campanulata) a number of delicate transverse muscles are present around the foot and trunk (fig. 27); by their contraction these portions of the body are compressed, and the body fluid driven forward to unfold the corona. In the corona this musculature is richly developed (figs. 27, 28), though the separate muscles are fine. Two sphincter muscles are present here, one close to the coronal margin and another behind it. Numerous slender longitudinal muscles connect these together and with the hypodermal thickening. The diaphragm has its own sphincter, and receives branches of the lateral and ventral longi-

tudinal trunk muscles; while the walls of the vestibulum have a rich network of muscles. There are three pairs of large visceral longitudinal muscles (figs. 22, 23, 25, 27, 28), a pair of dorsal (D.M.), of lateral (L.M.) and of ventral (V.M.) muscles respectively, attached anteriorly to the coronal margin, passing the whole of the trunk and in the foot converging together to form a muscle band which extends posteriorly as far as the proximal end of the peduncle (fig. 40); the cell bodies (Musc.C., fig. 28), and nuclei of these large muscle cells are placed within the foot. Probably the proventriculus has its proper musculature, thought it could not be determined; and the muscles of the coophageal tube have been already mentioned.

Nephridial system.—This is essentially the same in conklini (fig. 25), campanulata (28, 30, 41) and coronetta (figs. 22, 23). Opening into the posterior end of the cloaca is an unpaired, thin-walled contractile vesicle (Con.V.), and into this an unpaired contorted canal enclosed by a membrane. From the proximal end of this canal pass forward the two longitudinal canals, one on each side of the trunk, a little more ventral than dorsal in position. The anterior portion of each of these canals becomes convoluted, and this convoluted portion is thicker than the rest of the duct with a narrower lumen, and somewhat contractile. It is only by continued study of compressed living individuals that the bendings and interlacings of these very transparent canals can be determined. Anteriorly each longitudinal canal gives off an anterior and a posterior ductule. Each anterior ductule divides close to the lateral wall of the corona into three secondary ductules, each terminating in a single flame cell (Fl.C.). The posterior ductule passes caudad to about the region of the esophageal tube on the side of the body, then divides into two secondary ductules, a shorter dorsal one ending in a flame cell on the side of the mastax, and a longer ventral branch terminating in another flame cell on the latero-ventral aspect of the trunk. In conklini I could not ascertain the mode of union of the ductules with the lateral canals, on account of the large number of those floating corpuscles within the body cavity which greatly obscure the nephridial organs. F. ambigua (fig. 21) differs from the preceding species in having six flame cells and ductules on each side of the body, i.e. an additional one near the anterior end of the longitudinal duct. Ambigua also differs from the other forms in having the membranous tube which encloses the posterior unpaired canal much longer than in the other species; but I did not have sufficient material to determine its exact length. Only in coronetta (fig. 23) is there an anterior commissure joining branches of the anterior ductules of the two sides of

the body. In *Floscularia* the flame cells are readily found, but it is very difficult to find all the connections of the ductules and tubules.

Cilia are found only within the flame cells, as a long intracellular tuft or flame, and these terminal cells appear entirely closed off from the body cavity; they have also no connection whatsoever with the lateral antennæ (as one observer had supposed).

Organs of problematical significance.—In conklini there is found a large transparent structure (Gl., fig. 25) immediately below the hypodermis (and peripheral to the other internal organs), at the junction of the corona and trunk. It is lobed and forms here a ring just beneath the hypodermis, and attached to it. It appears to be gelatinous. Probably this is a glandular structure, and the dorsal gland of Stephanoceros may be homologous.

In *coronetta* a vesicular dorsal, hypodermal structure (*D.Gl.*, fig. 23). probably a gland, is found just below the dorsal sense-organ.

Nervous system, sense-organs.—In all the species the cerebral ganglion (Cer., figs. 20, 22, 23, 25, 28) lies deep below the hypodermis, on the dorsal surface of the vestibulum; it is elongate from side to side and composed of numerous small nerve cells. The nerves arising from it were studied most thoroughly in campanulata. In this species (figs. 28, 32) the ganglion seen from the side shows quite clearly a distinction between a dorsal and a ventral portion. From the dorsal side two nerves pass anteriorly to the dorsal sense-organ (D.Sens,O.), and a single nerve in the median line posteriorly to end on the hypodermis. From the anterior edge of the ventral portion of the ganglion a large nerve fiber passes antero-laterally to each lateral sense-organ (L.Sens. O.); two smaller nerve pairs pass posteriorly from its posterior margin: and from its lateral margin a pair of large nerves on each side downward and backward along the surface of the proventriculus. nerve fibers could be seen more clearly in life than upon stained preparations; methylene blue staining gave no positive results.

In coronetta there is found on the sides of the corona a single pair of small red eyes (E., figs. 22, 23). In some adult individuals of ambigua (fig. 20), but not in all, were found a number of eyes, up to five in all, on the dorso-posterior part of the corona; these have an irregular arrangement, and each consists of a few large red pigment granules. Campanulata and conklini have no eyes in the adult stage. All the species possess an unpaired dorsal (D.Sens.O., figs. 20, 22, 25, 28), and a pair of lateral sense-organs (L.Sens.O., figs. 20, 23, 27, 28) (antennæ) upon the corona, each bearing a tuft of long sense hairs. In campanulata the dorsal organ (D.Sens.O., fig. 32) was found to consist of from

four to six hypodermal cells, the sense hairs of which project outward through an aperture in the cuticula.

Female genital organs.—In campanulata (Ov., figs. 27, 28), coronetta (Ov., figs. 22, 23) and conklini (fig. 25) there is a more or less rounded germarium upon the ventral surface of the trunk; its cellular lining is continued caudad as the oviduct (which serves also as an uterus), and the latter opens as an unpaired tube into the cloaca between the openings of the rectum and the nephridia (figs. 29, 30). The germarium consists for the greater part of its bulk of a syncytium of yolk cells with large nuclei (Yk.N.) and huge nucleoli; there are some fifteen or more of these cells. At one end of the germarium is a cap of cells with much smaller nuclei, which are ovogonia (Ovg.). As the latter increase in size they are pushed in succession into the oviduct, where the cleavage commences. In conklini and campanulata two or three large ova are found in the oviduct (uterus) at once, in campanulata never more than a single one. In ambigua the germarium has an entirely different form (Ov., figs. 19, 20); it begins proximally upon the dorsal left-hand side of the trunk, extends down that side, then across the ventral region to the right hand of the trunk, and at the latter point the mature ova are found in the oviduct. I could not determine, owing to lack of material, where the ovogonia are placed within this remarkable germarium.

Body cavity.—This lies beneath the hypodermis, is continued in the coronal lobes, and in the foot as far posterior as the peduncle. In it float masses of minute, brownish, non-cellular corpuscles, which vary in number in different individuals of the same species, and in conklini are always exceedingly numerous and very minute. They are dissolved by alcohol, and the larger of them often appear doubly refractive. They must be metabolic products, probably waste products, but I have never found them within the nephridial lumina. In ambigua when the animal is fully extended and somewhat compressed in life beneath the cover-glass, it appears as if these corpuscles flowed within special channels between the hypodermis and the infundibulum, and like Gosse (1862) I was at first inclined to believe that there existed here a subhypodermal vascular system. But further study showed that the apparent canals are not fixed structures but simply portions of the general body cavity.

The immature female.—This stage was studied particularly in ambigua, but the general characteristics are the same in all the species. This free-swimming stage (Pl. XIX, fig. 21), just hatched from the egg, has only an incipient corona and foot. The other differences from the

adult are mainly the following: Two red eyes (E) are present in all the species except in *conklini*. No coronal lobes are yet developed, but at the anterior end of the trunk is a thickened hypodermal ring bearing a row of vibratile cilia. On the ventral side of and just behind this ring is the mouth opening (M.), leading into a capacious infundibulum (from which a vestibulum has not yet become demarcated), the inner lining of which bears long cilia. It is important to note that these cilia lie within the alimentary tract, i.e., belong to its inner lining and thus cannot represent a cingulum. The thickened hypodermal ring becomes subsequently prolonged to form the coronal lobes, and the cilia of the infundibulum are at no time a portion of the corona. Above this portion of the alimentary tract lies a large dense mass, part of which may represent the cerebral ganglion (Cer.). The hypodermis of the foot consists of a few enormous cells. A tuft of cilia projects posteriorly from the posterior end of this incipient foot; and in its axis lies a hollow cylinder of cells enclosing a granular, elongate body, which may represent the gland (F.Gl.) which forms the peduncle. tuft of cilia at the posterior end of this embryonic foot was found, in a somewhat older stage of campanulata which had attached itself and developed a peduncle, to be still present and placed at the junction of the foot and peduncle; in the figure (Pl. XXI, 38) the cylindrical cellular mass within the foot probably represents embryonic muscle cells of the foot. The remaining organs are essentially as in the adult.

The mature male of F. campanulata.—The males of this species were found in November and the first half of December; the male eggs, as in other Rotatoria, are more numerous and smaller than the eggs which give rise to females. The mature male (Pl. XXI, fig. 36) in size and general structure, disregarding the sexual organs and the alimentary tract, shows a great similarity to the immature female. lacks an alimentary tract entirely, and I was unable to find a nephridial system, though undoubtedly the latter must be present. The thickened hypodermal ring at the anterior end of the body bears a single ring of long, vibratile cilia, and in the projection of the trunk anterior to this ring lie two semicircular, dorsal, red eyes (E.). The foot (F.)is very short, without peduncle. The hypodermis (Hyp.) is thickened and with an irregurlaly scalloped inner contour. A dorsal sense-organ (D.Sens.O.) is well developed. In the anterior region of the trunk lies a large mass which may in part represent a cerebral ganglion (Cer.). The genital organs consist of a huge sperm sac (Sp.S.) connected with a cirrhus (Cir.). This sperm sac is filled with spermatozoa, and its walls thin except at one point on its dorsal surface which is thickened; probably this thickening represents the germinal epithelium and therefore the testis (Test.) proper. A curled thick-walled tube, the cirrhus, follows the sperm sac; its lumen, the vas deferens (V.D.), is very narrow. A thin-walled short tube connects the posterior end of this cirrhus with the dorsal genital aperture; and within this tube beat long cilia which are attached to the posterior end of the cirrhus. The cirrhus may be protruded some distance out of the genital aperture, and probably serves as an intromittent copulatory organ. On the ventral side of the cirrhus, in close attachment to its wall, is a large dense body (Gl.) with an axial pyriform clear space; I interpret this to be a gland, and the clear space to be its duct. Just posterior to this gland is a lobed body projecting into the body cavity, bearing on one of its surfaces long cilia which beat in the body cavity. No further structures were observed in the living animal.

The copulation was not observed. In a number of the females studied at the time the males occurred were found spermatozoa, from one to about a dozen in each female. All seen were within the body cavity of the female and none in any portion of her genital tract. The spermatozoa (Pl. XX, fig. 33) are relatively huge lumbricoid cells, very elongate, the more vibratile end of which appears to correspond to a thick flagellum; they are exceedingly active and twist about within the female, and within the sperm sac of the male, like animated corkscrews.

# CONCLUDING REMARKS.

The family of the Flosculariidæ includes the three genera Floscularia, Stephanoceros and Apsilus. Leidy's description of Acyclus is too incomplete to allow us to determine whether this form should be included in the group also. Apsilus differs quite markedly from both Floscularia and Stephanoceros (these two are very similar), but agrees with them in possessing an æsphageal tube, in the similar relations of the nephridial and nervous systems, and in the great similarity of the young. The immature females just hatched from the egg have the foot bearing a tuft of cilia at its distal end.

The general characteristics of the family are as follows, based upon the few species already known anatomically: The anterior portion of the trunk is expanded to form a capacious coronal cup, the free margin of which is prolonged into lobes (Stephanoceros and most species of Floscularia), or is without lobes (Apsilus, Floscularia edentata Collins and pelagica Rousselet). The whole free margin of the corona constitutes the boundary of a large mouth aperture. Cilia are absent upon the corona in Apsilus. In Stephanoceros they are arranged

Tn in numerous oblique rows upon the surfaces of the coronal lobes. Floscularia there is in most species a single row of cilia upon the lobes or on both the lobes and the interlobular coronal margin; in a few there are two rows upon the coronal margin (pelagica Rousselet, hoodii Hudson, cucullata Hood, trilobata Collins). All these cilia are preoral; they constitute, therefore, a trochus, and there is no postoral row (cingulum) on the external surface of the body behind the mouth. In fact, no postoral ciliary ring occurs, for the diaphragm of Stephanoceros and Floscularia, which bears a row of cilia, and on that account was homologized by Hudson and Gosse with the cingulum of other Rotatoria, belongs to the intestinal tract and not to the coronal margin at all. In the young of Apsilus and Floscularia the mouth is ventral instead of terminal, as in the adult, and the anterior region of the alimentary tract is ciliated, these cilia not persisting to the adult stage. The diaphragm separates in Stephanoceros and Floscularia an anterior infundibulum from a posterior vestibulum, both without cilia; in Apsilus there is no diaphragm and no distinction of two chambers, and also no ciliation. In two species of Apsilus, in Floscularia and Stephanoceros an esophageal tube is present. On the vestibulum follows a non-ciliated proventriculus, the posterior end of which is specialized as the mastax; next, a ciliated stomach; then a non-ciliated posterior intestine, then the short rectum opening into the cloaca. The intestinal ciliation is thus limited to the diaphragm, the stomach and (in some species of Floscularia) to the rectum.

The foot is well developed in all but Apsilus; in this genus it is larger in the young than in the adult, so has probably degenerated. Only in F. chimæra Hudson does the foot terminate in two toes (it is doubtful whether this form belongs in the family). In all other forms it terminates in a single peduncle (except in Floscularia atrochoides Wierzejski). The foot is strongly contractile, but not retractile into the trunk. The nephridial system is essentially alike in all three genera, likewise the nervous system; no ring nerves have been found in the coronal margin, and there is no subcesophageal ganglion. A dorsal and a pair of lateral coronal sense-organs are always present, and an additional pair of lateral ones in Apsilus. The germarium and oviduct are unpaired; the germarium is small and rounded in most species, but much elongated in Apsilus bucinedax (Forbes) and Floscularia ambiqua Hudson. Distinct foot glands are absent in the adult; the only glands connected with the alimentary tract are one pair of stomach glands. A gland around the dorsal sense-organ is found in some forms.

The young are free-swimming, but it is the rule that the adults live permanently attached within a gelatinous tube. The exceptions are the pelagic species Floscularia pelagica Rousselet, atrochoides Wierzejski, libera Zacharias. Since some of these swim carrying a gelatinous tube, it is probable that they were derived from sedentary forms. All the known species are restricted to fresh water, except two which are eurhyaline.

The sexes are dimorphic, and the small males represent individuals arrested in their development (they have considerable resemblance to immature females), and also degenerative in structure (shown by the absence of the alimentary tract).

The whole structure is bilaterally symmetrical; even the unpaired dorsal sense-organ has a pair of nerves, which, as Zelinka has correctly argued elsewhere, points to its original paired condition. The radiality evinced by the arrangement of the coronal lobes is referable to the sedentary mode of life.

Finally, in contradiction to most other *Rotatoria*, in most species that have coronal cilia, these do not serve to create food currents, but are stiff and more like pseudopodia.

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# EXPLANATION OF PLATES XVIII, XIX, XX, XXI.

The figures, with very few exceptions, are freehand drawings, each constructed from a considerable number of sketches or various details of structure. The degree of magnification is not uniform. These figures were made with the pen and were not reduced in size, which will account for occasional irregularities in the lines. The following is the significance of the abbreviations employed:

A.Sens.O., antero-lateral sense organ. B.C., body cavity. c.c.1, c.c.2., contractor coronæ primus

and secundus.

Cer., cerebral ganglion. Cir., cirrhus (penis).

Cl., cloaca.

Cl.Ap., cloacal aperture.

Con.V., contractile vacuole. C.T., compressor trunci. Cut., cuticula. D.A., dorsal coronal arm or lobe. d.c., deflexor coronæ. D.Gl., dorsal gland. Dia., diaphragm. D.M., dorsal longitudinal visceral muscle. D.Sens.O., dorsal sense organ. d.tr. I-IV, depressor trunci primusquartus. E., eye. F., foot. F., foot. F.Gl., foot gland. Fl.C., nephridial flame cell. Ful., fulcrum inci. Hyp., hypodermis. Inf., infundibulum (coronal cup). L.A., lateral coronal arm or lobe. l.c., levator coronæ. L.-C.M., longitudino-circular muscle. L.M., lateral visceral longitudinal muscle. L.Sens.O., lateral sense organ. M., mouth aperture. Man., manubrium mallei. Mast., mastax. Musc., muscles.
Musc.C., muscle cell body. N., nucleus. N.c., nerve cell. N.com., nerve fiber commissure. Neph., nephridial canal. Neph.C., nephridial cell.

Neph.com., nephridial commissure. N.f., nerve fiber. O., Ovum. Oes., œsophagus Oes.T., œsophageal tube. Ov., germarium. Ovd., oviduct. Ovg., ovogonium. Ped., peduncle of foot. P.Int., posterior intestine. Prov., proventriculus. R.c. I-VI, retractor coronæ primussextus. Ram., ramus inci. Rec., rectum. R.M., retractor mastacis. Sph.An., sphincter ani. Sph.C. I–VIII, sphincter coronæ primus-octavus. Sph.tr. I-VI, sphincter trunci primussextus. Sp.S., sperm sac. Stom., stomach. Stom.Gl., stomach gland. Test., testis. Tub., gelatinous tube. Un., uncus mallei. V.A., ventral coronal arm or lobe. Vac., vacuole. V.D., vas deferens. Vest., vestibulum. V.M., ventral visceral longitudinal muscle. x., cuticular ridge. Yk.N., necleus of yolk cell.

#### PLATE XVIII.—All the figures refer to Apsilus vorax.

Fig. 1.—Dorsal view; this and figs. 2-4 represent fully expanded individuals. Figs. 2, 3.—Lateral (from the right side) and ventral views respectively, the details of the alimentary tract not shown.

Fig. 4.—Newly hatched immature individual, about one-third the size of the adult, the musculature and cuticula not shown.

Fig. 5.—Left half of the mastax viewed from above.

Fig. 6.—Cerebral ganglion and its nerves, sense-organs, anterior portion of

the nephridia, and contiguous muscles.
Figs. 7, 8.—Two consecutive transverse sections of a cerebral ganglion, camera drawing.

# PLATE XIX, Figs. 9-18.—Stephanoceros fimbriatus.

Fig. 9.—Trunk seen from the left side, only the proximal portions of the coronal arms and the foot shown, details of the mastax not drawn. In this as in figs. 10 and 11 only the larger muscles are delineated, and those only in part.

Fig. 10.—Dorsal view of trunk.

Fig. 11.—Oblique ventral view of anterior trunk region with a portion of the

coronal lobes.
Figs. 12, 13.—The distal ends of two coronal arms, the first on dorsal and the

second on lateral view.

Fig. 14.—Distal end of foot with its peduncle. Fig. 15.—A nephridial flame cell.

Fig. 16.—An entire individual enclosed within its gelatinous tube, ventral view, the larger longitudinal muscles shown.

Fig. 17.—Germarium, from a stained preparation. Fig. 18.—Mastax, postero-dorsal view.

Figs. 19-21, Floscularia ambigua.

Fig. 19.—Germarium seen from left side of the body. Fig. 20.—Dorsal view of anterior body region, musculature and corona cilia not shown.

Fig. 21.—Immature individual pressed from the egg, seen from the right side; the musculature and mastax not drawn.

Plate XX, Figs. 22-24.—Floscularia coronetta.

Figs. 22, 23.—Lateral (from the left side) and dorsal views of anterior portion of the body; the cilia of the coronal lobes not drawn, and only a portion of the musculature.

Fig. 24.—Posterior end of foot with its peduncle.

Figs. 25, 26.—Floscularia conklini.

Fig. 25.—Anterior portion of body seen from the left side, mastax not drawn, and only a portion of the musculature.

Fig. 26.—The entire animal with its gelatinous tube, from the right side.

Figs. 27–35, Floscularia campanulata.

Fig. 27.—Oblique ventral view of anterior trunk region, the nephridia not shown.

Fig. 28.—View from the left side; in this figure as in the preceding the coronal cilia are not shown.

Fig. 29.—Germarium from a stained preparation, camera drawing.
Fig. 30.—Germarium, oviduct and posterior portions of alimentary tract
and nephridia of an immature individual.

Fig. 31.—Antero-ventral view of the corona. Fig. 32.—Somewhat oblique lateral view of the cerebral ganglion and its

Fig. 33.—A spermatozoon from body cavity of a female. Figs. 34, 35.—Esophageal tube in two positions of movement.

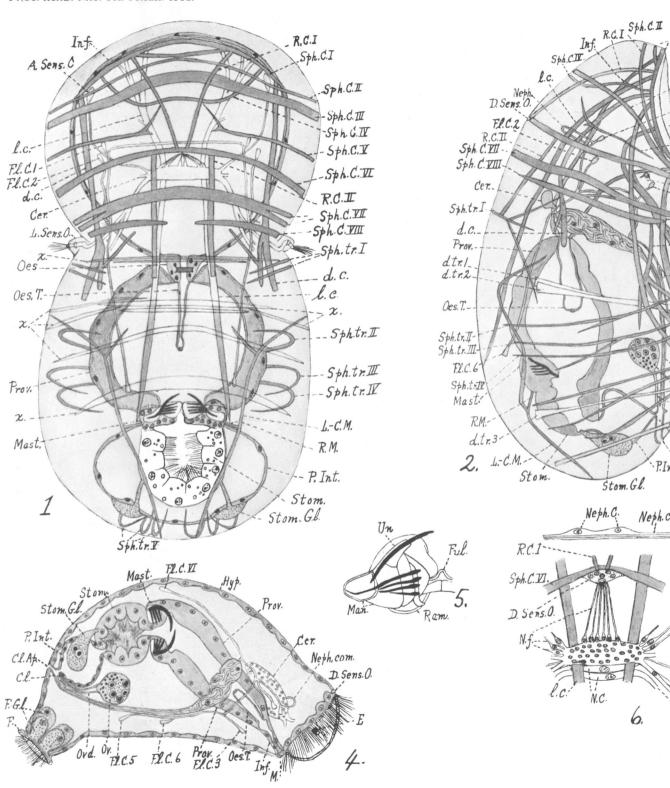
# PLATE XXI.—All the figures refer to Floscularia campanulata.

Fig. 36.—A male from a tube of a female which contained 8 ova. This mature male measured not more than the length of the dorsal coronal lobe of the female. Viewed from the right side, the musculature and cuticula not drawn, from life.

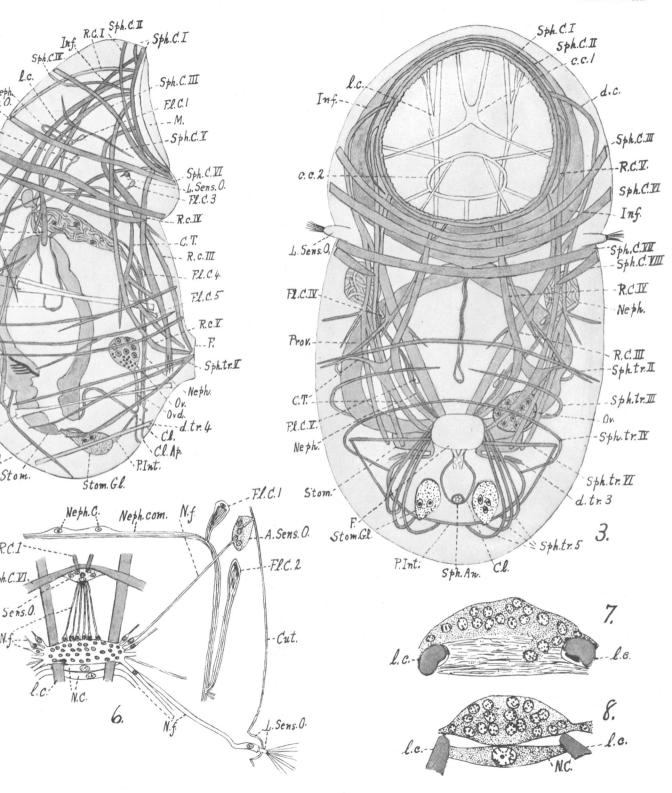
Fig. 37.—An entire individual within its gelatinous tube. Fig. 38.—Foot of an immature female, only about one-quarter the adult size, but attached.

Fig. 39.—Mastax, dorsal view, muscles not drawn.
Fig. 40.—Posterior end of foot and its peduncle of an adult individual.

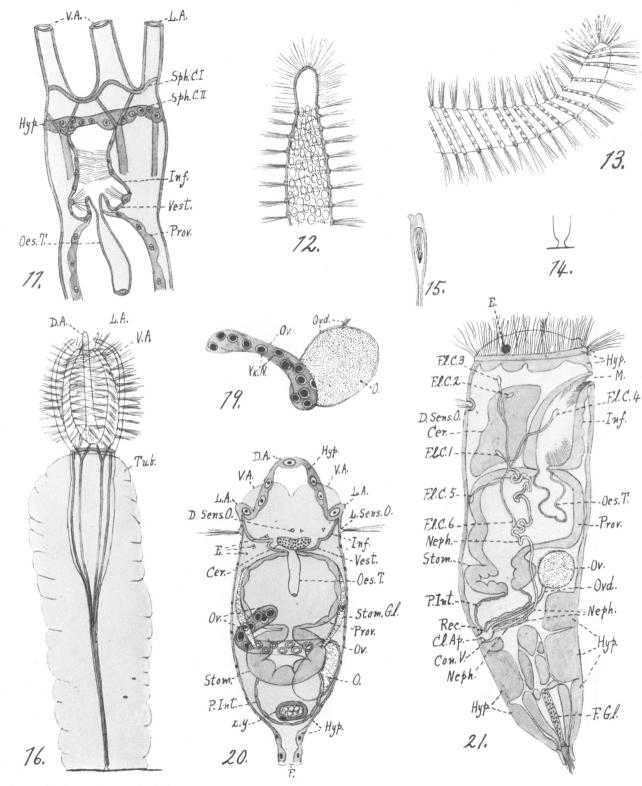
Fig. 41.—Nephridium of the right side of the body.



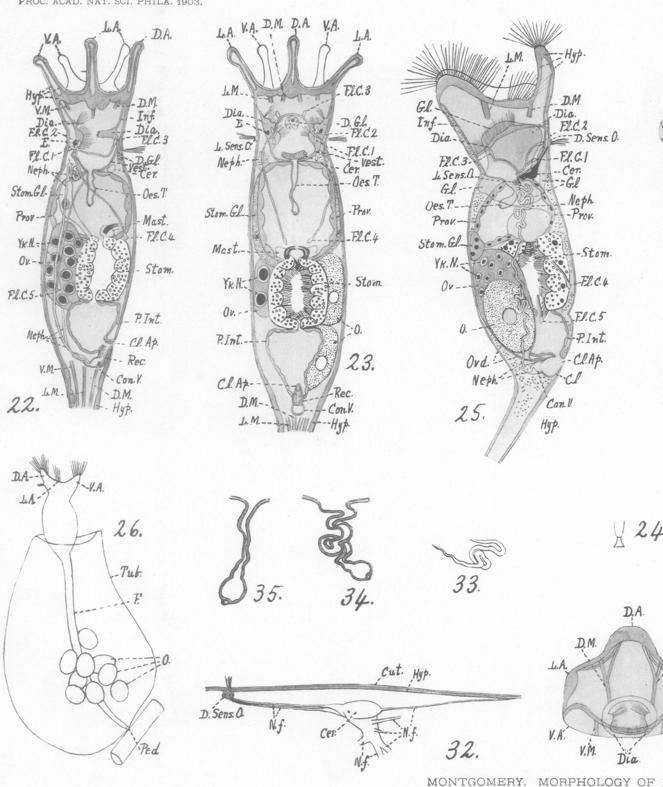
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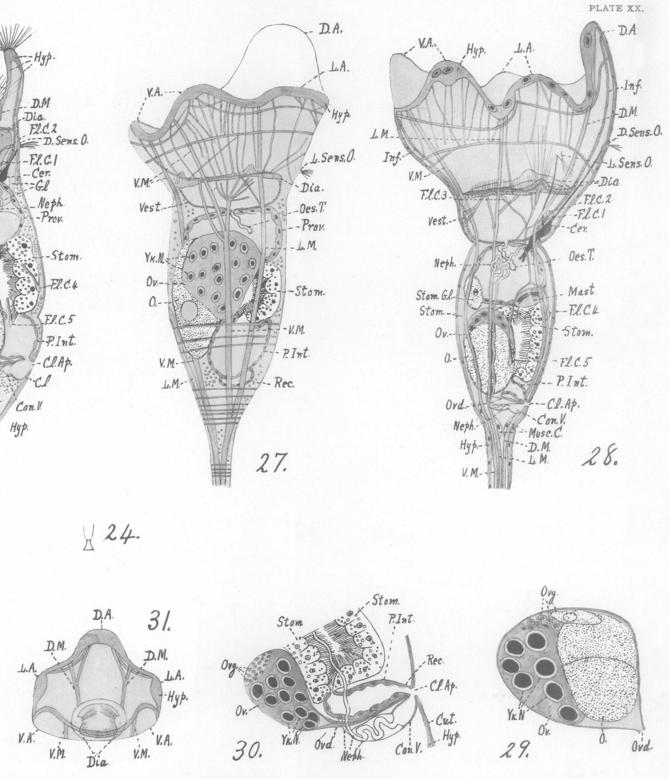


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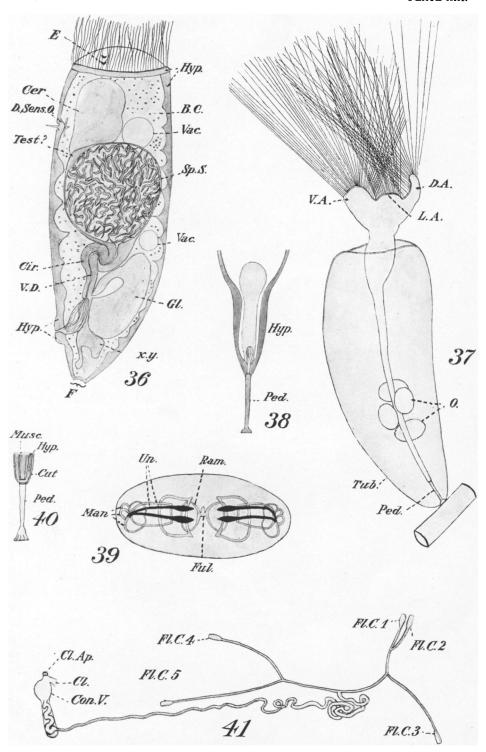


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